PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE, ARTS, AND LETTERS
VOL. XLIX, 1964 (1963 MEETING)

ZOOLOGY

VALVE ACTIVITY IN FRESH-WATER PELECYPODS [1]

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INTRODUCTION

FRESH-WATER pelecypods in their natural environment exhibit varying amounts of movement. Some species of clams which characteristically inhabit gravelly riffles of streams probably travel little or not at all once they are established. Others, in different water and bottom conditions, respond to seasonal and other fluctuations by burrowing or moving from one location to another (Baker 1928; Pennak 1953). Pelecypods move typically by extension and retraction of the muscular foot, with attendant opening and closing of the valves. This valvular activity was chosen as the criterion of clam movement partly for convenience, but also because it was surmised that this activity was an indication of much of the dynamic organization of the animal. Feeding, respiration, excretion, locomotion, and other functions may be carried out somewhat independently in the clam; however, all these probably influence, to some degree, the position and movement of the valves.

The main purpose of this study, then, was to describe the valvular activity of certain fresh-water clams. Especially sought was evidence of biological rhythmicity as manifested by the abduction and adduction of the valves. The effects of temperature and light were observed.

Three species of clams in the family Unionidae were investigated: *Anodonta grandis, Lampsilis siliquoidea*, and *Anodontoides ferussacianus*. The first two species were collected from Silver and Windover lakes respectively and the third from the south branch

[1] This study received support from the Michigan Academy of Science, Arts, and Letters and from the National Science Foundation, Grant No. G-21933. Grateful acknowledgment is made to Alma College for the use of laboratory facilities.

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of the Tobacco River. All were collected in Clare County in Lower Michigan during June 1962.

Materials and Methods

Each clam was supported by a stationary mount clamped to one valve and was suspended in a three-gallon aquarium. A wire was cemented to the other valve and this articulated with an ink-writing lever. The latter recorded valve movement on a standard kymograph drum which was geared to a speed of one revolution every six days. 12 such setups were put into operation. Four specimens of each of the three species were used. Strained beef and beef heart were fed at irregular intervals and apparently maintained the animals in a healthy condition.

One clam of each species was placed in constant dark (DD), one in constant light (LL), and one in 12 hours of light beginning at 6 A.M. followed by a 12-hour period of dark (LD). With one exception, each clam remained in the same light regime throughout the entire experiment. However, each spent approximately 10 days in each of three different temperatures: $11 \pm 1°$ C, $22 \pm 1°$ C and $29 \pm 1°$ C. At any one time at a given temperature the valve activity of all three specimens of the same species were recording on the same drum. All temperatures given are water-temperature readings. A fourth specimen of each species was placed under conditions of natural light in the laboratory at a room temperature of $23 \pm 2°$ C. With the exception of the LD chamber at 29° C, where it was necessary to use a $7\frac{1}{2}$ watt bulb to prevent an excessive temperature increase, illumination for the other LD animals came from 15-watt bulbs at a distance of approximately one foot. Laboratory ceiling lights were used for LL animals at all three temperatures. Natural light entered through north windows; the clams never received direct sunlight.

To each record of activity was added a time base which was divided into three-hour intervals. The actual length of the activity trace in excess of the baseline was measured by the use of a small calibrated wheel. These values were used to compute the mean activity curves for each of the eight three-hour periods in a day. Actual distances that the valves moved were small; therefore, these were amplified by the lever system for greater accuracy in measurement. Although the lever arrangement for each of the setups was l in Clare County in Lower

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identical, a small difference in the position of the lever fulcrum may have caused the amplitude to vary slightly. The recordings were made between June 12 and August 23, 1962.

We decided that valve opening after several hours of closure constituted the best measure of the onset of activity. We recognized that other parts of the recorded activity might contain significant information, but we felt unable to identify them with confidence.

Results and Discussion

It was found, after several days of recording, that characteristic elements in the tracings could be recognized. Some patterns were peculiar to the individual clam, and others seemed characteristic of the species. For example, all animals showed periods of complete closure. The clam may remain closed a majority of the time, as with *Anodonta*, or only for brief periods, as shown by *Lampsilis*. Valve closure was usually preceded and/or followed by vigorous activity which suggested effort on the part of the animal to flush away debris or excrement or to effect increased gaseous exchange across gill surfaces.

The thin-shelled *Anodonta* opened and closed rapidly at more or less regular intervals. *Anodontoides* exhibited a characteristic pattern in which the valves open wide just after a closure. During the rather long periods where the valves were open, there was a two-to-three-hour cycle in which the extent of gap changed. On this shorter cycle were five to seven smaller changes in valve position; this gave the appearance of waves upon waves. The valves of *Lampsilis* typically remain closed for much shorter periods than those of *Anodonta* and *Anodontoides*. Also typical of *Lampsilis* were vigorous flushing or ventilating movements accompanying the opening and closing of the valves. This species has a curious steplike rather than continuous movement when changing the position of the valves.

The animal whose activity was recorded for the longest period was a specimen of *Anodonta* (Fig. 1). This animal experienced two different lighting conditions and three temperature changes. During the early part of this record there was indication of rhythmic activity (Fig. 1). The mean period from one valve opening to the next during the time from June 12 to July 2 was very close to 24 hours. The vigorous activity usually occurred during the night. Unfortunately, there was an interruption in the recording from

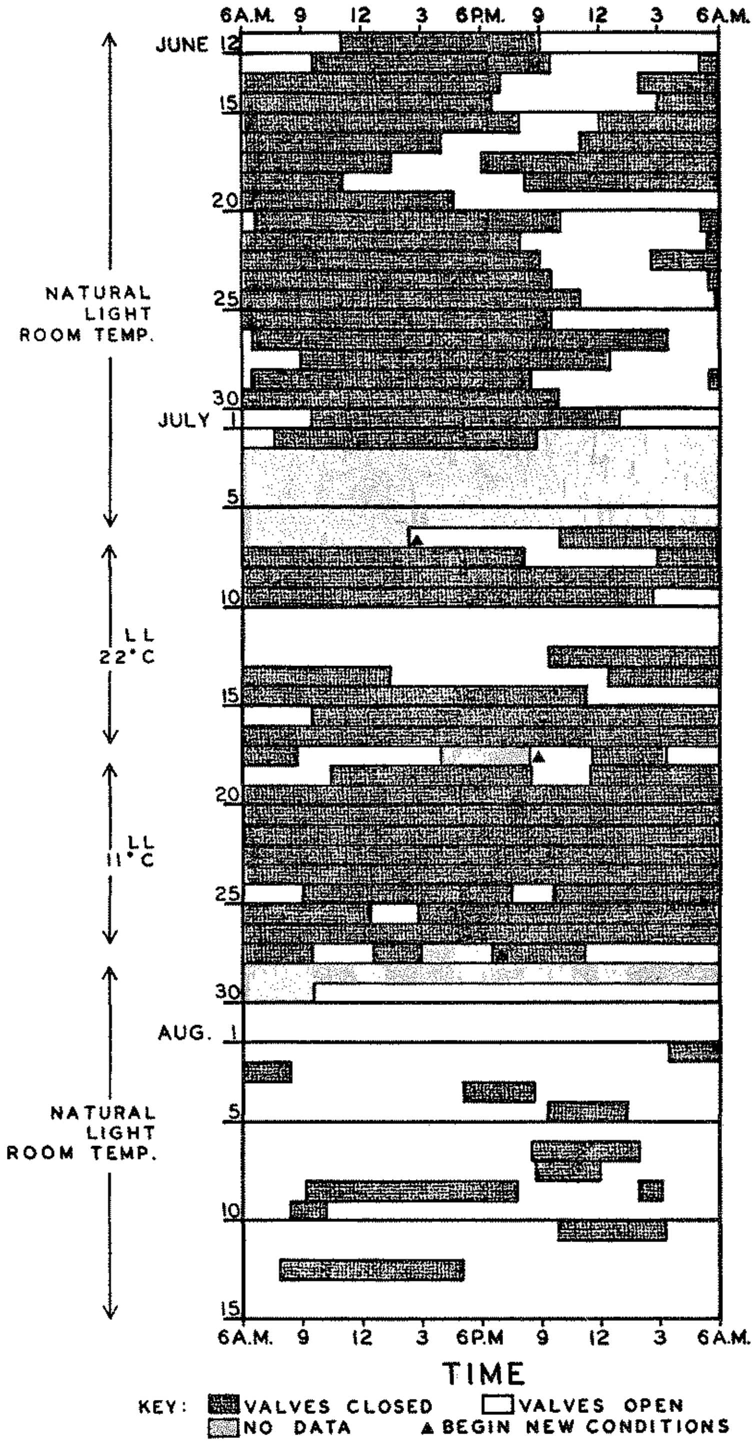

Fig. 1. Valvular activity of *Anodonta* from June 12 to August 15.

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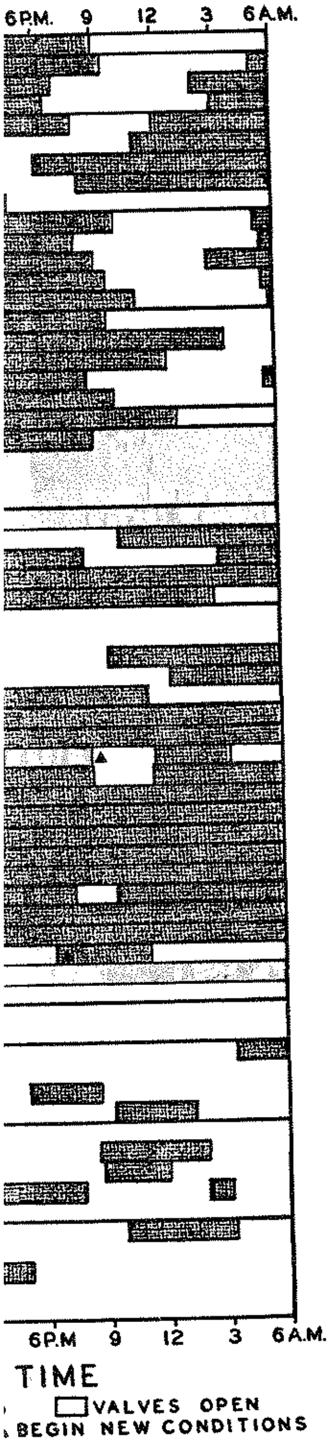

from June 12 to August 15.

July 2, until the animal was placed in LL at 22° C on July 7. From that time until the record stopped on August 15, the clam did not exhibit any consistent repeated activity. Fig. 1 shows that the clam did not respond to daylight as it had in the early recordings, after its exposure to LL.

Another specimen of *Anodonta* exhibited an 8-hour cycle followed by a 24-hour cycle in DD at 22° C. From these records and personal impressions gained from the total record, it is suggested that this species possesses a period of valve opening of approximately 24 hours, with occasional shorter cycles of 8 hours. On several occasions regular patterns of valve closing and opening were observed, but these would disappear for no detected reason. The most regular recordings were obtained from animals in natural conditions or LD, but the period was not always 24 hours. A mean period of 39 hours over 16 consecutive valve openings was shown by *Lampsilis* in natural conditions. On another occasion a different individual of the same species in LD averaged 42 hours over four consecutive openings.

In an early record of *Anodontoides* in natural light, periodic peak activity of approximately 25 to 26 hours appeared. This suggests the possibility of a lunar influence. The method by Brown (1955) was used to analyze the data. Peak activity was exhibited later and later in the dark portion of consecutive days until the peak occurred near dawn. The interval to the next peak was shortened so that it appeared again during the early part of the next dark period. This process was repeated for three cycles of approximately 6 days each. Later records showed a gradual lengthening between distinct closing, and finally only variation in extent of opening without complete closure was shown.

In all three species these periodic movements appear to be easily disrupted. Change from one temperature or light condition to another, as well as unknown influences during apparently constant conditions, seemed to repress periodicity. Perhaps vibration from opening and closing of the heavy doors of the constant temperature rooms or fluctuation in atmospheric pressure were factors in this regard. No record of barometric pressure was kept, and the authors view this as an unfortunate omission.

The data in Figs. 2, 3, and 4 show total mean values of valve movement for the three species investigated. Values were given for each of the eight 3-hour periods into which the day was divided.

Generally, there was only one period of relatively high activity per day. A specimen of *Anodontoides* in LD was the most active animal of those tested. In general, the gross activity of this species exceeded that of the other two tested; the preponderance of the movement occurred either during the subjective day (LL and DD) or during the dark period (natural light and LD) of the alternating regimes. *Anodonta* and *Anodontoides* in natural light and LD were most active from 6 P. M. to 6 A. M. *Anodonta* and *Lampsilis* in LL and DD generally showed less total activity and no obvious preference for any particular period. *Anodontoides,* in LL and DD, exhibited more valvular activity during the subjective day. The typical peak of activity for almost all clams in LD and natural light occurred during the night.

A rationale for the timing of peak activity of *Anodontoides* in LL and DD conditions is suggested. Two "cues" to the animal may operate to cause peaks of activity; the first is endogenous, initiating the gradual accumulation of energy and is triggered by the second, an exogenous cue. According to Bethe (1946) the slow accumulation of energy will discharge when it reaches a maximum. It can also discharge earlier if stimulated by an external excitatory process. Without the latter, a greater period is necessary for sufficient energy to accumulate before discharge. In our case of *Anodontoides* in LL and DD (Fig. 3) there is no external light cue, and a period of approximately 12 hours may be required before spontaneous discharge level occurs. With *Anodonta* and *Lampsilis,* the endogenous chronometer-like cue may exist but never reaches a threshold level where spontaneous discharge occurs in the absence of light change; hence, reduced and arhythmic movement results. Bunning's remarks (1960) concerning the possible existence of a relaxation oscillation may be applicable to the findings from these latter genera. A single stimulus was necessary to initiate the oscillation. In LL there was no dark period or relaxation phase, and in DD no tension phase induced by light. Therefore, repeated high activity periods were not initiated.

The influence of the three temperatures upon the period from valve opening to valve opening is shown in Table I. For each temperature-light combination, two numbers may be seen. The one in parentheses indicates the number of valve opening cycles included, while the other is the mean value of these cycles, in hours. There are certain obvious shortcomings in treating data in this

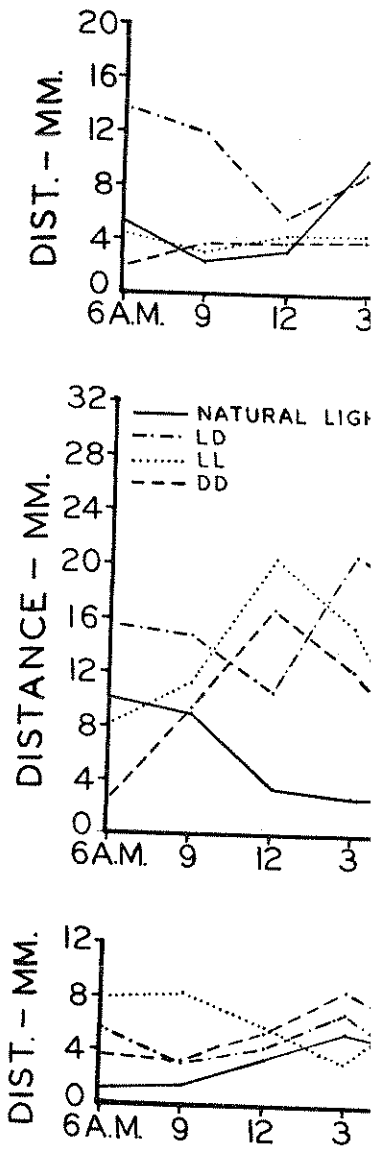

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FIG. 4 (bottom) *Lampsilis*.

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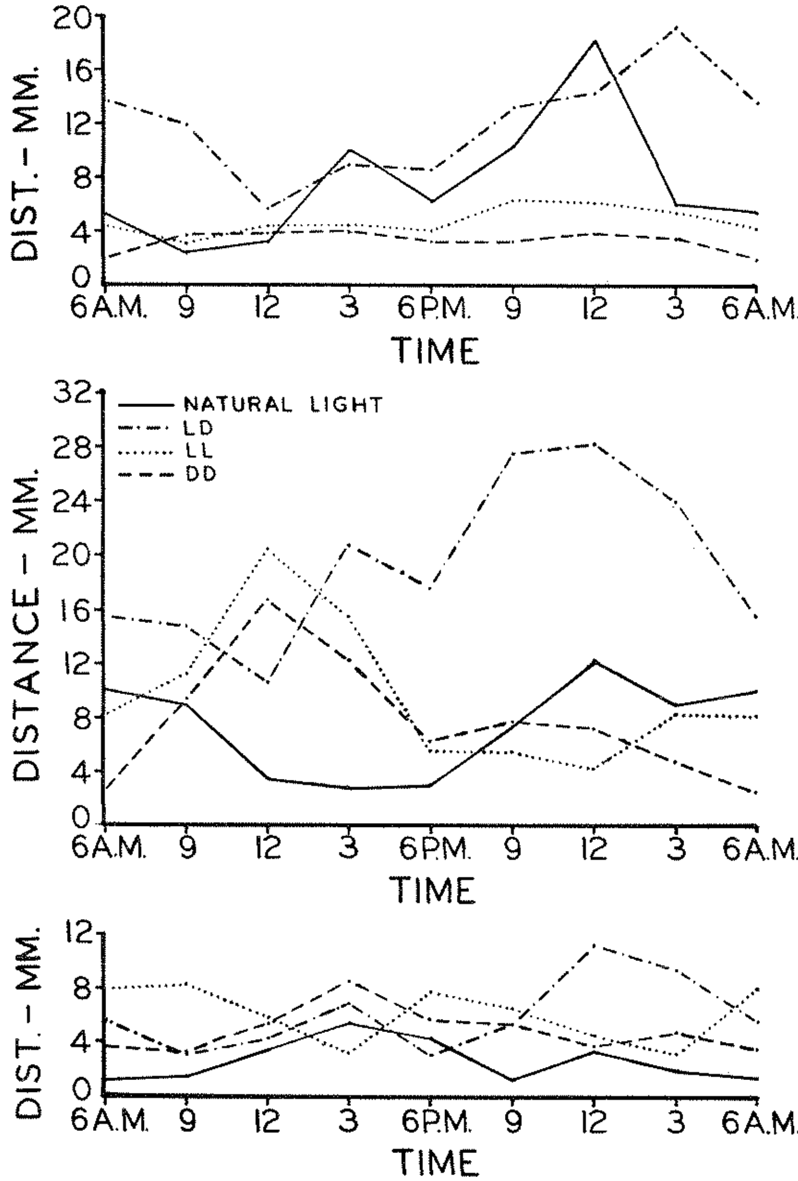

FIGS. 2-4. Mean distances of recorded valve movement over the entire period of investigation. FIG. 2 (top) *Anodonta*, FIG. 3 (middle) *Anodontoides*, FIG. 4 (bottom) *Lampsilis*.

manner: the amount of actual valve movement is not shown; the valves might remain completely closed with sporadic openings, or they might exhibit vigorous movement with short closures. Further, mean values do not reveal sequences where regular openings oc-

TABLE I

Mean Periods (in hours) from One Valve Opening to the Next

		Light			
Species	Temp.	LL	DD	LD	Daylight (23 ± 2° C)
Anodonta	11° C	44 (5)	22 (4)	55 (3)	
	22° C	58 (4)	13 (19) a	32 (5)	24 (20) *
					18 (47) *
	29° C	12 (4)	7 (6)	27 (19) b	
				23 (18) †	
Anodontoides	11° C	23 (10)	remained closed	38 (4)	
	22° C	26 (17)	49 (8)	61 (8)	31 (22) c
					25 (18) †
	29° C	remained open until death			
Lampsilis	11° C	74 (7)	26 (4)	46 (4)	
	22° C	37 (4)	31 (7)	42 (4)	41 (21) d
	29° C	22 (8)	31 (7)	23 (10)	

a-d lists (below) actual consecutive periods, in hours, from opening to opening.

a. 10.5, 16, 7, 9.5, 9, 9, 7, 6.5, 8, 8, 7, 8, 8, 8, 13.5, 15.5, 48, 26, 27.5.

b. 13, 12, 15.5, [92], 10.5, 16, 15.5, 34, 17, 29, 26, 23, 19, 29, 24.5, 24.5, 39, 31.5, 35.5

c. 26.5, 23.5, 25, 29, 17, 21, 28, 24.5, 26, 31, [87], 26, 26, 22.5, 26, 21.5, [67], 27, [253], 30, [50], 19

d. 42, 29, 24, 18, 31.5, 74, 50, 33, 24, 37, 39.5, 31, 69.5, 51, 48, 40, 39, 40, 91.5, 30, 26

* Different animals.

† The data immediately above this number were recalculated without including the atypically high valves shown in brackets at the bottom of the table.

curred. Nevertheless, the fact that a closure occurred where the valve muscles showed no overt activity for a period is thought to be of significance. Parts of the record made just after moving the animal and during other major disturbances were not included.

Anodonta and *Lampsilis* generally opened and closed their valves more frequently with increase in temperature. The reaction of

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	Light				
			Daylight		
D	LD		(23 ± 2° C)		
(4)	55	(3)			
(19) a	32	(5)	24	(20) *	
			18	(47) *	
(6)	27	(19) b			
	23	(18) †			
ained	38	(4)			
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(8)	61	(8)	31	(22) c	
			25	(18) †	
until death					
(4)	46	(4)			
(7)	42	(4)	41	(21) d	
(7)	23	(10)			

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opened and closed their valves emperature. The reaction of

Anodontoides to temperatures revealed the upper and lower limited tolerance. All specimens of *Anodontoides* tested in 29 ± 1° C succumbed within 3 days. The animal in DD at 11° C failed to open during the period lasting 11 days. *Anodonta* exhibited a thermal-death temperature intermediate to *Anodontoides* and *Lampsilis*, in that two animals in a preliminary test lived only 5 and 7 days at a temperature of 29 ± 1° C. A single specimen was still living after 23 days in a temperature of 27 ± 0.5° C.

The valve-opening periods for the specimen of *Anodontoides* in daylight showed a mean of 31 hours; however, if one were to discount the four longest periods (50, 67, 87, 253 hours) the remaining ones fall close to an average of 25 hours. This is also true for the specimen of *Anodonta* in LD. If the 92-hour period is discounted, a 23-hour periodicity remains. These atypically long valve periods, 253 hours for example, suggest that the laboratory environment may be deficient or abnormal in some important way. The *Anodonta* in DD at 22° C showed a very rhythmic period of 8 hours for 4 days and then changed suddenly. Throughout the remainder of the record it never returned to this rhythmicity. This leads to a recommendation that, in further studies, effort should be made to recognize basic natural habitat requirements and to provide for them in the laboratory situation. Another parameter (previously mentioned) which might be helpful in the interpretation of the results is barometric pressure. A lever, recording activity of the foot, would be desirable to show periodicities in locomotory activity. Possibly this would shed light upon certain characteristics of valve movement which have remained uninterpreted to this point.

Conclusions

Where there is a light cue as in LD and normal daylight, the valvular activity is greatest during the dark period. *Anodonta* and *Lampsilis* showed no peak activity when placed in constant light or dark; *Anodontoides* exhibited a peak during the subjective day for these constant conditions. *Anodonta* and *Anodontoides* did not survive exposure to 29° C. *Anodonta* and *Lampsilis* generally showed valve openings to increase in frequency with a rise in temperature, while the reverse was indicated in *Anodontoides*. On several occasions cycles of valve openings approximated periods of 8 hours or multiples thereof. 8-hour periods were shown by *Anodonta* in DD at 22° C. *Anodontoides* exhibited 24-hour periods in LL at 11° C and 22° C and also in daylight. *Anodonta* also showed 24-hour periodicity in LD at 27° C and in daylight. A 40-hour period was shown by *Lampsilis* in LD at 22° C and in daylight.

In all three species valve movement occurred when approximately the same period was repeated for several cycles. In all cases these patterns were disrupted by a change of light or temperature, and often they would disappear for no apparent reason. The sporadic occurrence of prolonged activity and valve closure suggested that more attention should be given to the simulation of natural conditions of the clam's environment.

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